

IV. *On several instances of the Anomalous Development of the Raphe in Seeds, and the probable causes of such deviations from the usual course of structure, especially in reference to Stemonurus (Urandra of Thwaites), with some Prefatory Remarks on that Genus.* By JOHN MIERS, Esq., F.R.S., F.L.S. &c.

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IN a recent Number of Hooker's Journal of Botany (vol. vii. p. 211), Mr. Thwaites has recorded a new genus, of which he gives the characters under the name of *Urandra*. This he refers to "*Olacaceæ*, tribe *Icacineæ*." I have read over his description with the utmost care, and am obliged to say that I perceive no difference whatever in the characters of *Urandra*, and those I have detailed of *Stemonurus*, to which genus he confesses it is closely allied, differing only in all its flowers being fertile, in its small, not pulvinate, stigma, and in the structure of its fruit. The character founded on the constancy of the hermaphrodite flowers in the plant which he describes, cannot be considered of the smallest generic value, because this circumstance has been shown to exist not only in some species of *Stemonurus*, but in the contiguous genus *Platea*, in which, although some of the plants are unisexual, others are frequently hermaphrodite. I have also shown that the stigma in *Stemonurus* (*Gomphandra*, Wall.) is small, and not large and pulvinate as it had been described, but that it becomes subsequently immersed in the epigynous gland which crowns the ovary, a circumstance evidently not observed by Mr. Thwaites; and that it is this gland which assumes a pulvinate form on the summit of the fruit, and not the stigma, which may always be seen hidden in a small central depression of the cushion. There remains therefore to be considered only the structure of the fruit; and Mr. Thwaites's details of the ovary, fruit and seed in *Urandra*, closely agree with what I have observed in *Stemonurus*. In this genus, as in all others of the *Icacinaeæ*, where the ovule is usually unilocular, the cell is always excentrically placed on one side of the pistil, the point of suspension of the ovules not being from the summit of the cell, but constantly inclined against the side on the line of the displaced axis of the ovary: the lobes of the stigma are always two or four, thus showing *primâ facie* that the ovary is normally bilocular, and that the two ovules observed in the cell are really attached, near its summit, to the dissepiment, which, owing to the abortion of the other cell, appears to form the wall of the ovary. I was fortunate enough to meet with the proof of this conclusion in a ripe fruit of the closely allied genus *Pennantia*, where the ovary is usually unilocular as in *Stemonurus*; but in the instance alluded to, the fruit was regularly two-celled, and only one seed was perfected in each cell, the remaining abortive ovule being still visible on the dissepiment at the point of attachment of each seed; this partition was of thin texture, and the nourishing vessels proceeding from the base formed a longitudinal nervure in the line of its axis, extending thence to the point of attachment

of the seeds near the summit of the cells. Here we have the most positive proof of the normal structure of the whole family, and this fact ought to be held in view in those cases which ordinarily occur, as in *Stemonurus*, where one of the cells has become obliterated by partial abortion.

The able botanist who has given us the details of *Urandra*, has had the advantage of examining the fruit in a living state, and describes it to be a somewhat fleshy drupe with a subligneous putamen, its solitary seed consisting of an embryo formed of two small cotyledons and a superior terete radicle loosely seated in the upper part of a longitudinal cleft or cell in a large albumen, which is thus nearly divided into two almost equal plates, by the intervention of two cellular strata that line this cavity, and whose margins nearly reach the testa on every side. This exactly corresponds with what I have observed in *Stemonurus*, and the same features are confirmed by Dr. Wight in his 'Icones,' under *Stemonurus* (*Gomphandra*) *polymorphus*, where they are well delineated in plate 954. figs. 11 & 12, and where the chink above mentioned is shown distinctly in fig. 13. Mr. Thwaites examined the texture of the nucleus of *Urandra* under the microscope, and he describes the albumen to consist of cells, radiating from the more central tissue to the periphery of the seed; he states that the two strata lining its cavity are formed of cells similar to those of the albumen, but differing in containing no amylaceous granules: he considers them to be organically connected with the albumen, but I succeeded most certainly in separating them as easily as the integuments, and still preserve them in this state. At the time I published my Monograph of the *Icacinaceæ*, I had been able to examine only a single drupe of *Stemonurus*; but I was fortunate enough afterwards to obtain another seed, through the kindness of the late Major Champion, which I analysed, and found that a portion of the embryo, in the first instance, had been partially eaten by a small insect, then observed within the cavity, so that the real cotyledons were gone, and I found a portion of the radicle, situated in the manner I had described, in the upper part of the axis of the albumen, and placed at one extremity of the two thin membranaceous strata described by Mr. Thwaites. I naturally concluded, by analogy, that these were the cotyledons; they occupied the same position, and were about the size of the foliaceous cotyledons I have delineated in *Mappia fœtida*, and as these are figured by Dr. Wight (Icon. 955. figs. 10 & 11) under *Stemonurus fœtidus*. In my second analysis, made soon after the publication of my Memoir on *Stemonurus*, I discovered the embryo entire, with small cotyledons, just as Mr. Thwaites has shown them; my attention was now, therefore, drawn to the consideration of the nature of the two membranaceous strata, well described by that botanist. The result of this examination, and my correction of the form of the embryo, would consequently have been given in the forthcoming volume of my 'Contributions,' where the details of *Stemonurus* and all other genera of the *Icacinaceæ* are figured. I am, however, glad of this opportunity of rectifying my previous description, and of adding a drawing of my analysis of the seed.

Another circumstance mentioned by Mr. Thwaites calls for observation. In *Stemonurus* the albumen of the seed is covered by the ordinary delicate membranaceous inner integument, and this again is invested by a very thin testa, which is intimately agglutinated to it, and which is marked by fine hexagonoid reticulations. The raphe, prominent upon

the testa, and which by pressure leaves a corresponding groove on the surface of the albumen, is singular in its form, on account of its retroversion in the manner I have detailed, both here and in my Monograph of the genus. Its nature does not appear to have occurred to Mr. Thwaites, for he describes it merely as "a whitish raised line, which is very conspicuous on the outside of the seed, passing quite round it lengthwise, and consisting of a fillet of spiral vessels lying between the two thin coats or layers of the testa." The nature of this fillet is soon ascertained by tracing it to its origin, and I have again referred to the parts of my two analyses which I have preserved, and these confirm my previous inference. As its form and position involve other considerations of some importance, it is desirable to describe it more in detail. On examining the putamen, which is the lignified endocarp of the fruit, we find it of an oval form, slightly flattened on one side, along which is observed a longitudinal groove, in which is imbedded a thick cord or bundle of fibres, which is easily raised from the channel, and is found to penetrate an aperture in the upper extremity of the groove: some fibres proceeding from the stigma here join it, and the cord now reduced to a thread, after its passage through that aperture into the cell, becomes attached to the testa of the seed, on a small protuberance near its apex; it then assumes the features of a prominent line upon it, and descends along one angle of the dorsal face of the seed, to near its base, then curves round this, and ascends along the other angle of the same face, to a hollow in the summit, beneath the apical protuberance just mentioned, where it disappears, describing in its course a horse-shoe, or rather an oval curve: and this is the "whitish raised line" described by Mr. Thwaites. The nourishing vessels are thus distinctly apparent throughout their entire course, from the external base of the putamen to the vanishing point of the thread just described, in one continuous line: the external portion of this cord is evidently the placental axis of the dissepiment of the normal bilocular ovary, for in the 2-celled and 2-seeded fruit which I have mentioned, where the seeds were separated by a distinct partition, this same cord was seen imbedded in the line of its axis, and became furcated on arriving at the summit, each branch passing through a double aperture into the two cells, where it attached itself to the apex of each seed, and continued in its course as the "whitish raised line" of Mr. Thwaites: this thread therefore bears the character of a raphe; but as its form is very peculiar, it is well to compare it with the same organ in other genera of this family.

The development of the seed in *Stemonurus* is precisely similar to that in *Pennantia*, as I have elsewhere shown, agreeing even in the same relative size, shape, and position of the embryo, differing only in the singular extension of the raphe, and the presence of a large vacuity in the centre of the albumen, lined with thin pellicular plates. In *Pennantia*, as in other genera of the *Icacinaceæ*, the raphe originates as in *Stemonurus*; but its course is along the middle of the dorsal face, and it loses itself at the opposite or cotyledonary extremity of the testa, according to the law of anatropal development: in the latter genus, contrary to general rule, the descent of the raphe is along one side of the seed, and, after crossing the lower part, it ascends up the other side, to near the point from which it started, and is lost in the integument, close to the extremity of the radicle: the raphe in this course, which is always inclined a little towards the dorsal face, leaves

by its pressure a corresponding groove close to the periphery of the albumen: the margins of the large cavity in the albumen, in which the much smaller embryo is suspended, also correspond with this line of circuit of the raphe, so that the albumen along this line is reduced to a very thin substance, and consequently is nearly separated into two parallel slabs. In *Stemonurus* I could not perceive the indication of any chalaza at either extremity of the inner integument, and there exists a more intimate union of this integument with the testa, which are both of delicate texture. In *Pennantia*, on the contrary, a distinct chalaza is visible at the cotyledonary extremity of the inner integument at the vanishing point of the dorsal raphe: the same exists in *Mappia*, and probably in all other genera of the *Icacinaceæ*. Mr. Bennett (Plant. Jav. rar. 131) quotes the observations of Mr. Brown and of M. Brongniart to show that the eversion of the raphe upon the dorsal face of the seed is of frequent occurrence in *Celastraceæ*, *Rhamnaceæ*, *Aquifoliaceæ*, and *Caprifoliaceæ*, and is fully confirmed by his own experience in the seeds of *Euonymus* and *Rhamnus*, where it is frequently everted, though often only laterally displaced; and he entirely adopts the opinion of Mr. Brown, that this eversion of the raphe in no way militates against the universal law of anatropal development; for on examining these occurrences at an early stage of their growth, he invariably found the ovule with its raphe on the ventral side, or that next the placenta, and he observed that its subsequent appearance on the opposite or dorsal face, is due to an evident torsion of the upper extremity of the raphe, or short funiculus, during the increment of the seed, and not to any original development. The eversion of the raphe in the *Icacinaceæ*, together with a similarity in other essential points of structure, strongly prove the close affinity of this order to the *Celastraceæ*, *Aquifoliaceæ*, and other families which I proposed to unite with it into one general alliance (the *Dryales*), nearly allied to the *Rhamnaceæ*.

In the above-mentioned structure in *Stemonurus*, a curious deviation from the usual development of anatropous seeds occurs. In the organization of most of its parts there exists, as before mentioned, a perfect analogy with that found in *Pennantia*: the seed is albuminous, and the radicle of the embryo is superior and pointed to the hilum; but while in *Pennantia* we trace the raphe in a straight line to the opposite or cotyledonary extremity, as in ordinary anatropous seeds, we find in *Stemonurus*, owing to the singular retroversion of the raphe (that is to say, its continuation beyond the point where it ought to have terminated, and its subsequent ascent to the summit—to the point of its disappearance near the hilum), that this unusual circumstance is not attended by a corresponding change in the position of the embryo, and offers a paradox difficult of explanation. In ordinary cases, the ovule makes a semi-gyration on its centre, thus producing a complete inversion of the embryo and its integuments, all moving together in accordance: but do we not see, from the course of the raphe in *Stemonurus*, an indication that a complete gyration or double anatropal action of one or both of the integuments has occurred, while the embryo at the same time has effected only a half-gyration, or simple anatropal movement? How can we otherwise account for the peculiar form of the raphe in this case? I will recur again to this point when I come to speak of other developments which appear to offer much analogy with this phenomenon.

In order to prepare the way for this investigation, it is of some interest to determine

the nature of the two thin membranaceous plates, or cellular strata, that line the cavity of the albumen, as before described, and I think these may be referred, with little doubt, as we shall see in other well-authenticated cases, to the existence of a large persistent embryo-sac which has not been absorbed, as it usually is in most seeds. In the case in question, at the upper extremity of this cavity, the embryo only one quarter of its length is found, and here the radicle, pointing upwards, terminates in a long mucronate point, which is a kind of suspensor, by which it is pendent in the mouth of the cavity, and where it is enveloped in a small quantity of glutinous matter, which lines the internal surface of the sac. Instances of the existence of this cavity in the axis of albuminous seeds are not unfrequent, but the discovery that it originated in the persistence of the embryo-sac is due to Mr. Brown (App. King's Voy. p. 21).

The first consideration that arises is the question whether the existence of this persistent embryo-sac has any necessary connexion with, or has had any share in producing the phenomenon of the retroversion of the raphe, and the inversion of the embryo in regard to it, in the manner before stated; whether the two latter unusual circumstances are independent of each other, or whether they are necessarily connected. The only method of forming any conjecture on this head, is to search for facts that have any collateral bearing on the question. In *Diospyros* we meet with a parallel case of a large cavity in the middle of an albumen, which is open at the hilum, and is in like manner lined with an adherent embryo-sac; the embryo is found in the outer end of the much larger cavity, the end of the radicle almost protruding out of its mouth: the albumen is deeply divided into numerous lamelliform folds, as in *Anona*, and is covered by two thin integuments, of which the inner one is plicated within the interstices of its lamellar clefts, while a distinct raphe, adhering to the outer integument, proceeds along a groove formed in one of its marginal sides, from the basal hilum to the summit, or opposite cotyledonary extremity, where it disappears. We have here therefore a parallel instance of the existence of an open cavity in the albumen, lined with the embryo-sac, but this circumstance is accompanied by the presence of an ordinary raphe, while both the seminal tunics and the embryo have gone through the usual process of anatropal inversion.

In *Anona* we meet with a complete peripheral raphe, as in *Stemonurus*, but the embryo-sac has disappeared; there is therefore no cavity, as the embryo lies tightly imbedded in the substance of the albumen, and the radicular end of the embryo, with a very short mucronate point, or suspensor, is directed to the spot where the raphe, after completing an entire circuit round the periphery of the seed, disappears close to the hilum. In this instance we find that a complete gyration of the original tunics, as indicated by the raphe, and only a semi-gyration of the embryo, have taken place; thus offering a perfect analogy with the structure of *Stemonurus*, excepting the presence of the embryo-sac and its accompanying cavity. These two instances seem to prove that the presence of this albuminous cavity and the complete gyration of the raphe do not necessarily accompany each other, and they leave us as much in the dark as ever, regarding the cause of the phenomena observed in the seed of *Stemonurus*.

In *Opuntia* we have another example of a completely annular raphe, but the embryo, imbedded in a small quantity of albumen, is quite campulitropal: the raphe after com-

pleting its circuit penetrates the testa through the diapyle, at a point where the two extremities of the recurved embryo are brought into close contiguity, although separated by a peculiar inflexion of the inner integument, close to the chalaza, so that this integument is here bisaccate, one recess receiving the end of the radicle, the other the extremities of the cotyledons. In this case there appears no vestige of any embryo-sac, and although the raphe is completely cyclotropal*, only the cotyledonary or chalazal extremity of the embryo has accompanied it in effecting an entire revolution, while its radicular end has remained anatropal, having experienced only a half-gyration. This example therefore, although analogous in some respects, affords no assistance towards an explanation of the phenomena of *Stemonurus*.

In the *Plumbaginaceæ*, we have a remarkable instance of the complete gyration of the ovule under very different circumstances: in an early stage it is simply inverted according to the ordinary course of anatropal development, that is to say, a semi-gyration of the entire ovule on its centre, accompanied by the usual extension and adhesion of the placentary sheath or future raphe on the ventral side of the primine: subsequently a farther growth of the placentary sheath, or rather of the funicular attachment of the ovule, takes place, which becomes prolonged into a free cord, which, by its growth, again pushes the ovule onward, so as to turn it farther round on its centre, another half-revolution: the result is, that the funicular cord, arising in a free state from the base of the ovary, attains the summit of its cell, and from it the anatropal ovule is suspended; its cotyledonary or chalazal extremity thus returns to its normal position in regard to the carpel, after having performed a complete revolution on its centre, at the same time that it has only effected a half-revolution in respect to the point by which it was originally attached to the placenta. The embryo during all these changes continues perfectly straight; the placentary sheath or first expansion of the funicular cord remains adherent to the primine in the usual manner, while its subsequent extension is permanent as a free cord, so that the ovule, though strictly and simply anatropal in respect to the raphe, is in fact cyclotropal in regard to the carpel. This development is again different to that observed in *Stemonurus*, inasmuch as the embryo has remained stationary, or what is almost tantamount, has made a complete gyration on its centre. One parallel circumstance however exists in the form of the albumen, which, as in that genus, consists of two parallel plates united on their periphery by a thin annular zone corresponding to the commissure of the cotyledons.

In *Diospyros*, to which I have before alluded, the embryo, which remains in its original sac after the expulsion of the redundant amniotic secretions, appears to have preserved its relative position in regard to the integuments and raphe, and to be truly anatropous. It would however be desirable to ascertain, by the examination of fresh seeds, whether it offers any indication of a suspensor. I conjecture from the appearance of the dried seed, that a portion of the sac will be found to protrude from the mouth of the albuminous cavity which it lines, and from its great tenuity to have withered away, for I have always

* By this term, I propose to distinguish an ovule, where its chalazal point, and with it the raphe, effects a complete cyclical gyration: it is an extension of the campulitropal where the same point makes $\frac{3}{4}$ ths of a revolution, while anatropal it completes $\frac{1}{2}$, and in amphitropal only $\frac{1}{4}$ of a revolution.

found the end of the radicle extending a little beyond the mouth of the cavity: this conjecture is confirmed by the drawings of Gärtner (De Fruct. tab. 208). A similar persistence of the embryo-sac, and its forming the lining of a large cavity in the albumen, which is thus nearly separated into two parallel plates, and the occasional protrusion of this sac beyond the limit of the albumen, occur also in *Strychnos* and *Ignatia*, as may be seen from the figures given by Gärtner (De Fruct. tab. 189). The protrusion of a portion of the embryo-sac, and with it of the radicle, in the manner above conjectured to exist in *Diospyros*, is known to occur in *Myzodendron*, where it is well figured by Dr. Hooker in his 'Flora Antarctica,' plate 104. fig. 18 & 19; and in plate 105. fig. 17, 18 & 19*. A singular example of the persistence of the embryo-sac is afforded in *Marantaceæ*: this occurs in the genus *Thalia*, where two large vacuities are seen in its copious albumen, on each side of the embryo: these are the persistent sacs in which two abortive embryos had existed: this curious fact was first recorded by Mr. Brown nearly fifty years ago (Prodr. p. 307): it is one of the few instances that occur, where several embryo-sacs are generated in the same ovule.

In regard to the origin of the albumen in seeds, it was shown by Gärtner (*loc. cit.* Introd. 138), and Mr. Brown confirms it as a well-established fact (Linn. Trans. x. 36), that it is merely that condensed portion of the amniotic fluid which remains unabsorbed by the embryo at the termination of its growth. This excessive portion of the fluid is generally expelled from the embryo-sac (quintine, *Mirbel*), and is deposited and consolidated in the cellular tissue of the quartine, which lines the tercine (nucleus, *Brown*) when it constitutes the albumen, and in ordinary cases the sac becomes absorbed without leaving any trace of its existence. Besides the instances of its permanence just given, its existence under other peculiar circumstances was first shown by Mr. Brown, in the *Nymphæaceæ*, where a portion of the redundant amniotic fluid forms a separate and second albuminous deposit, immediately surrounding the embryo, which he has aptly named the vitellus, and which in the ripe seed is found lodged in an exserted portion of the embryo-sac: it is therefore always seen at one extremity, outside of the great mass of the ordinary albumen: when this occurs, it is accompanied by the appearance of a long tubular vacant space in the axis of the albumen which is the opposite extremity of the persistent embryo-sac, of which the other portion containing the vitellus is a continuation. This has been shown to exist among *Dicotyledones*, in the *Nymphæaceæ*, *Cabombaceæ*, *Saururaceæ*, *Piperaceæ*, &c., and in several cases among *Monocotyledones* (Appendix, King's Voy. p. 21). A very excellent illustration of this occurrence may be seen in the admirable work of Dr. Asa Gray (Gen. Pl. Un. St.), where evidence of its presence is shown in the seeds of *Nymphaea*, *Nuphar*, *Cabomba*, and *Brasenia*, in pl. 38, 39, 43 & 44. Mr. Brown observes (*loc. cit.* p. 22), "that the albumen, *properly so called*, may be formed by a deposition or secretion of granular matter in the utriculi of the amnios" (embryo-sac) "or in those of the nucleus itself" (tercine or quartine); "or lastly, that these two

* Schleiden (Linnæa, xi. 526. tab. 11. figs. 12, 13) has shown the curious fact, that in *Ceratophyllum* the principal portion of the embryo is developed outside of the embryo-sac, which in the ripe seed remains investing the plumule, and enclosed within the cotyledons; a small quantity of albumen is deposited in the embryo-sac around the plumule, but none is formed outside of the large cotyledons, which are invested only by a simple thin integumentary covering.

substances" (amnios and nucleus) "having these distinct origins, and very different textures, may coexist in the ripe seed, as is probably the case in *Scitamineæ*." In that family the embryo is enclosed in a fleshy vitellus, and this again is surrounded by albumen: owing to the difference of texture and consistence of the vitellus, its albuminous nature has been denied by some botanists. I have however met with an instance of a double albumen in *Boldoa fragrans*, a Chilean tree belonging to the *Monimiaceæ*: here the principal oval mass of the kernel of the seed consists of fleshy albumen apparently formed by two distinct deposits: the rather small embryo is seen with its cotyledons spread out quite flat by pressure, and as if they were seated astride upon the summit of the inner mass of the albumen, with its short radicle standing upwards; and the whole is enclosed within another concentric portion, much softer in substance, and formed of oily granules of much larger diameter than the close cells of the main inner portion, which is whiter, more dense, opaque, and fleshy, and from which it is easily separable in every part. Dr. Lindley (Veg. Kingd. p. 298) gives a good sectional analysis of this seed, but he has evidently not noticed the difference of the two kinds of albuminous deposit: the whole is covered by the proper inner integument, well distinguished at the extremity contrary to that where the embryo is seated, by a large dark chalaza, somewhat adherent to the outer tunic, which is recognized as being the testa, by its linear raphe, which is partly free near its origin. He justly claims for the *Monimiaceæ* a near affinity to the *Myristicaceæ*, for the form and position of the embryo quite correspond with those of *Pyrrhosa*, where, had its internal cavity been filled by a second deposit of albuminous matter, and were its outer coat not split into lamellar plates, we should have quite the seed of *Boldoa*: the whole plant of this latter genus, and especially its seed, bears a strong aromatic smell and taste, similar to that of the Nutmegs. The fact of the existence of a double albumen here fully realizes the prediction above quoted of Mr. Brown. This structure is of a generic, not of an ordinal character, for it does not exist in *Mollinedia*, a genus numerous in species, nor generally in *Citrosma*, although I have found it occur in one species of the latter genus. Brongniart also has demonstrated that albumen is generally formed in the quartine or cellular lining of the tercine, in which case he calls it the 'perisperm,' and at other times, though more rarely, within the embryo-sac, and then he gives it the name of 'endosperm*.' *Boldoa* hence possesses both a perisperm and endosperm, one concentric to the other, although the embryo-sac has entirely disappeared; but if the latter had remained persistent, if the endosperm had been absorbed, and the embryo and the perisperm had retained their present form and position, the seed of *Boldoa* would have been like that of *Stemonurus*, with the exception of the peculiar form and termination of its raphe.

In this stage of the investigation, it is desirable to recall to our memory the nature and origin of the embryo-sac. This vesicle, called by Gærtner the sac of the amnios, was first observed by Malpighi and Grew, who showed that it originated from that point of the ovule which I have called the ganglyode, or the point of vascular connexion of the primine and secundine with the main body of the ovule, and with the placental sheath, a point which afterwards becomes the chalaza of the inner integument, the diapyle in the

* Ann. Sc. Nat. xii. 265.

testa, and where the raphe terminates. Gærtner farther affirms that the amniotic fluid is secreted at this point of the gangylode, which is also the opinion of Mr. Brown (Linn. Trans. x. 37). This point is sometimes distinguished by a peculiar protuberance, within the cavity of the main body, which Mirbel calls the chalazal appendage (appendice chalazienne), and he says that at this point the embryo-sac is first developed. We are indebted to Mr. Brown (Append. King's Voyage) for nearly all the information we now possess respecting the nature and origin of the several parts of the ovule, and the changes they undergo during the growth and perfection of the embryo, and it is impossible to estimate too highly the importance and merit of these admirable observations, the truth of which is unquestionable. A large share of credit is due to M. Brongniart, who about the same time, and to M. Mirbel, who three years afterwards, contributed many important facts on this subject, all confirming the previous observations of Mr. Brown. The latter able physiologist brought together all this information in his two celebrated memoirs "On the Development of the Ovule," &c. (Mém. Acad. Sci. Paris, ix. p. 609 & 629): he there gives a regular nomenclature to the several parts of these developments, and reduces all the evidence into a beautiful system, which has been adopted by all, and which has remained unquestioned now for nearly thirty years; but true as it may be in a general point of view, the evidence I have now brought together will show that the laws considered so universal, fail in their application in many cases, perhaps in far more numerous instances than are here offered, or will at first be credited. The existence of the two outer tunics, the primine and secundine, had long been known; but their remarkably peculiar cupuliform shape, seen alone in a very young state, was first shown by Mirbel, and by him also the metamorphoses of the main body of the ovule, called 'chorion' by Malpighi, and 'nucleus' by Mr. Brown, who first explained its functions, were now more fully demonstrated. Mirbel, who called this 'nucleus' the 'tercine,' showed that it is lined with a peculiar tissue, which sometimes becomes transformed into another tunic, the 'quartine,' and which in *Statice* he describes as forming a completely closed vesicle. Another body, which he denominates the 'quintine,' is still farther developed in the interior of the quartine: this is the 'sacculus colliquamenti' of Malpighi, the 'amniotic sac' of Mr. Brown, the 'embryo-sac' of M. Brongniart, the point of origin of which has been noticed above; when this vesicle is wanting, which perhaps more frequently happens, it is then the quartine that becomes resolved into the embryo-sac. According to Mirbel, one end of this sac is attached to the point of the gangylode, while the other is fixed to the summit of the tercine or quartine: it gradually swells from top to bottom, thrusting away the tissue that surrounds it. Brongniart first noticed the fact of the descent of the boyaux of pollen-grains, through the stigmatic channel, but failed in tracing their farther course, and the mode of their action in effecting the fertilization of the ovule, a discovery due to Amici. According to the observations of more recent physiologists, it is now admitted, that in every case of fertilization of an ovule, the boyau of a pollen-tube descends through the stigmatic channel, and is conveyed through the apical orifices of the primine and secundine (the micropyle), and passing through the tercine, thus reaches the embryo-sac, in the summit of which is a small globular body, called by Meyen 'the primary utricle,' which body, consequent on its osculation with the boyau, subsequently swells and becomes

the nascent embryo. We will not here touch upon the still disputed point, whether the process of fertilization is the result of mere impact, or whether the boyau enters into the primary utricule; but will pass on to the fact admitted by all, that a new globular development subsequent to this action (the future embryo) is generated within the primary utricule, which is suspended within the sac by a delicate thread, often extending with the growth of the embryo in its young state: this is called the suspensor, which in some few instances becomes highly developed, though more frequently it is of no great length, sometimes remaining as a short distinct thread that terminates the extremity of the radicle, and which I have pointed out as existing in the embryo of *Stemonurus*. After the fecundation of the embryo, in the manner just mentioned, the embryo-sac as before stated, either by absorption, or by amalgamation with the surrounding tissues, generally disappears; but in some few cases, as we have seen, it remains persistent, and *Stemonurus* affords an instance of this occurrence.

I have entered into these details upon the nature and function of the embryo-sac, with the view of considering, whether a different amount of circumversion of this sac, respectively to that of the tunics of the ovule, may not have taken place in *Stemonurus*, which would thus account for the phenomena under consideration. May we not conclude, with some degree of confidence, that the embryo-sac has remained to form a cavity in the albumen, which has been copiously moulded around it, by amylaceous granules flowing from the redundant amniotic fluid deposited among the cellular tissue of the surrounding envelope? Has the embryo-sac in this case moved a half-revolution on its centre more than the coats of the ovule, or *vice versâ*? I cannot venture to affirm the fact, but the evidence is certainly presumptively in favour of such a conclusion. This indeed appears to me the only key to the solution of the paradoxical difficulty in question. It is, however, a point that can only be settled by observation on the growth and development of the ovule of *Stemonurus*, and as it involves a topic of great importance in a physiological and structural point of view, I would earnestly impress it on the attention of every botanist who has an opportunity of examining the ovule in a living state. In the mean time I call attention to the following evidence, which appears to favour this view of the question.

*Citrosma** will be found to offer some points of analogy with *Stemonurus*, as far as regards the cyclotropal form of the raphe and its termination close to the extremity of the radicle, or in other words, its anomotropal embryo. *Boldoa*, *Hedycarya*, and *Mollinedia*† severally have anatropous seeds, and those of *Ambora* and *Monimia* are described as having a similar development, so that *Citrosma* appears to be the only genus in this family where the raphe is cyclotropal and the embryo anomotropal. Here the raphe makes nearly an entire gyration round the periphery of the seed: it originates at the

* I take this opportunity of observing that the genus *Siparuna* of Aublet appears to differ in no respect from *Citrosma*: the form of its anthers and their mode of dehiscence were supposed to offer generic distinctions, but I found those of *Citrosma* quite agree with the description of Aublet; in habit and floral characters the one accords perfectly with the other.

† I may also affirm without hesitation that the genus *Tetratome* of Pöppig is identical with *Mollinedia* of the 'Flora Peruviana.' I have examined several species and made drawings and analyses of the living plants. I purpose at some future time to give the full characters of *Mollinedia*, *Citrosma*, and *Boldoa*, for which I possess ample materials.

hilum, near the bottom of the ventral margin of the nut, and at last arriving at the basal point, it terminates abruptly by penetrating the integuments: between this point and the hilum a very short space intervenes, which is obsoletely angular, and immediately at this angle, close to the margin, the small embryo is found imbedded in a large albumen, the radicle pointing outwards, and the two short fleshy cotyledons, greatly divaricated, being directed towards the vertex of the seed. Here then, as far as regards its direction with the hilum, the embryo is anatropal, having become inverted half a turn on its centre from its normal position, while the integuments have performed an entire gyration, by which the embryo is deprived of its anatropal characteristic. All the species of *Mollinedia* which I have examined have regular anatropal seeds, with one exception, where the raphe is cyclotropal, as in *Citrosma*. We have thus in *Citrosma* a verification of the fact observed in *Stemonurus*, the raphe terminating at a point exactly contiguous and corresponding to the radicle of the embryo, a fact quite incompatible with the laws of structure so beautifully expounded by Mirbel: it is a development that has hitherto been considered impossible, but I will proceed to show that these are not the only instances of the same occurrence we find in the structure of seeds.

In the development of the seed of the *Cucurbitaceæ*, we meet with a structure that offers much resemblance to the anomalies observed in *Stemonurus*; we find also other features, not only difficult of explanation, but contrary to all our ideas of the nature and function of the raphe. To aid us in the solution of these phænomena, we will first recur to the detailed account of the development and growth of the ovule of *Cucumis Anguria*, L., from the observations of Mirbel (Mém. Acad. Sci. Paris, ix. 621. tab. 1). The growth of the anatropal ovule is here shown in all its earlier stages, and we see that by the time of the fall of the flower, the micropyle of the primine and secundine becomes quite closed over the tericine; soon after which, a fine thread is observed to grow out of the micropyle, which was first noticed and described by Brongniart, in the ovule of *Pepo macrocarpus* and *Momordica Elaterium*. As the growth of the ovule proceeds, this tubular thread becomes covered by an envelope formed of cellular tissue: according to the drawing of Mirbel (*loc. cit.* tab. 1. fig. 10), it is a prolongation of the mouth of the embryo-sac; but Griffith says (Posth. Notes, 153), that although he had observed the same fact in several instances in *Cucurbitaceæ* and *Asclepiadaceæ*, he was never able to trace any connexion with it and the embryo-sac, and was rather disposed to consider this thread as formed by the boyaux or pollen-tubes, an opinion confirmed by the observations of Schleiden, and which appears the more probable conclusion, as no remainder of this thread is visible in the ripe seed. At the period above mentioned, the bottom of the embryo-sac breaks away from the ganglyode, becoming thus suspended by its apex, and the embryo is formed in its summit: there is no appearance in the raphe at this time to indicate any other change than the ordinary anatropal development. The same course of metamorphosis is said by Mirbel to occur generally among the *Cucurbitaceæ*. We will now compare these changes with the development found in the ripe seed, and I select my analysis of *Citrullus Colocynthis* as a fair example of the structure of the seed in this family.

Here the seed is obovate, much compressed, its hilum being an open slit along its

narrow basal extremity, which is enclosed in a short fleshy sheath, part of the funicle, from which it has broken away, and by which it is connected with the placenta, and suspended in the pulp of the fruit: a groove runs parallel with the margin on each face close to the periphery, forming in this manner a prominent zone all round the edge of the seed, which is broader towards the base, and which thus forms a short auricular expansion on each side of the hilum. On a former occasion (p. 92) I described the outer crustaceous tunic, hitherto considered as the testa, but which I shall prove to be of the nature of an aril, formed subsequently to the fertilization of the ovule, around its original integuments: it was there shown to be formed of three series of deposits, the epiderm, mesoderm and endoderm: the epiderm is a thin delicate membrane that covers the whole of the seed, and is extended beyond the hilum in the manner above-mentioned, as an extension of the sheath of the umbilical cord; the fleshy mesoderm has been before described, its numerous branching fibres being emanations from the bundle of simple vessels that fill the sheath of the funicular cord, and that surround the thread of spiral vessels proceeding from the placenta, that terminates in the raphe of the seed; the principal portion of the tunic is the endoderm, which is, in fact, a crustaceous compressed sac, enclosed in the above-mentioned vesicular terminal enlargement of the sheath of the umbilical cord; it forms a casing closed all round the seed, except at the hilum, where it has a long open slit, within the mouth of which is a considerable open space filled with pithy loose cellular tissue, which fills up this interval between the pointed extremity of the enclosed nucleus and the mouth of the crustaceous covering: there is no connexion whatever between any part of this crustaceous coating and the enclosed seed, which lies quite free within it, and fills up its cavity. The raphe, consisting of a number of spiral vessels enclosed in a delicate tube, is first seen to issue from the umbilical cord; it then finds its way through one of the basal auricular lobes of the endoderm, in which a channel is seen for its passage, after which it enters into the clear space between this crustaceous aril and the integuments of the contained seed, and under the form of a perfectly free delicate white thread, it runs all round the margin of the seed, forming a complete circle, until it again reaches the space within the mouth of the hilum, and when in the midst of the deposition of tissue before mentioned, it changes its course suddenly inwards, and terminates in the conical neck of the integument of the seed, by which the latter becomes thus suspended: this conical neck is of a dark brown colour, and is evidently the true chalaza of the integument. The covering of the enclosed seed is thin and membranaceous, generally of a greenish hue, is quite smooth and evidently composed of two, if not of three pellicular membranes, agglutinated into one thin integument. I have sometimes found this structure more clearly demonstrated where the nucleus has become withered from its full dimensions; it then appears as a large, perfectly transparent cyst, enclosing the diminished embryo, and by transmitted light displays the deeper colouring of the chalaza upon the inner membrane, which appears surrounded by another pellicle more transparent at this point: the presence of the spiral vessels in the suspending thread, up to the apex of the conical chalaza, is here perfectly distinct. At the other end of the integumental covering of the seed, the one contrary to that of its suspension, is seen another larger dark yellow arcole, over the cotyledonary extremity of the embryo, and therefore

at the point where, according to the laws of structure, the chalaza ought to be found in all cases where a raphe exists: it is precisely in the situation ascribed to the chalaza by Mirbel, in his figure before quoted of the ovule, after the formation of the embryo. It is however only a false chalaza, and is most probably a thickening of the mouth of the micropyle (exostome of Mirbel) of the ovular integuments, a circumstance of frequent occurrence in certain seeds; or it may possibly be ascribed to a scar of the embryo-sac, at the point where it has broken away from the gangylode, as figured by Mirbel (*loc. cit.* fig. 10. letter *f*). That it cannot possibly be the true chalaza, is most evident, because it has had no apparent connexion with the outer crustaceous tunic, which exhibits no corresponding scar or trace of any former connexion at this point; and still more obviously, because the raphe passes straight across it, without holding the slightest communication with it. The embryo, which has no albumen, fills the whole cavity of the integuments in the ripe seed, the radicle being directed towards the hilum and to the terminating point of the raphe, and its extremity being covered by the true chalaza; its cotyledonary extremity is in the opposite direction, terminating at the areolar micropyle or false chalaza. The fact of the existence of the free cord of spiral vessels as above-mentioned (the raphe), running between the outer crustaceous tunic and the inner integuments of the seed, was evidently known by Mr. Griffith, who notices it (*Posth. Notes*, p. 182); but he omitted to observe the passage of this thread over the areole, which has always been considered as the chalaza, and also its course round the entire periphery, as well as its termination at the radicular extremity of the membranaceous integuments: the presence of the true chalaza at this point also escaped his observation. I do not find any mention of this curious structure by any other botanist.

We thus observe the same phænomena existing in all the genera of the *Cucurbitaceæ* that I have described as being found in *Stemonurus*, *Anona*, and *Citrosma*, that is to say, where the cord of the raphe makes a complete circuit of the seed, terminating at the same time at the radicular point of the integuments, instead of the cotyledonary extremity, as it ought infallibly to do, according to the acknowledged laws of structural development. What has been the nature of the metamorphoses within the ovule, that have produced so manifest a deviation from the ordinary course of structure? We have it demonstrated on the high authority of Mirbel, that up to the period of the impregnation of the ovule, the raphe, the chalaza, and the primine and secundine (then agglutinated into one coat), had only performed a simple anatropal inversion from their normal position; but we find that in the interval between this period and the ripening of the seed, all these parts have experienced a farther circumversion, so as to complete an entire circle, while the embryo-sac, or at least the embryo, has retained the same position which it held at the period of the simple anatropal inversion of the ovule. Mirbel notices, at this last-mentioned period, the first indication of the growth of the arillæform coating over the primine, appearing at this epoch as two layers of cellular tissue coating that integument, and which he figures (*loc. cit.* fig. 10. letter *h*): these layers of tissue are unquestionably the rudimentary secretions that subsequently form the arillus, under the crustaceous appearance of a testa, for which it has always hitherto been mistaken: it is doubtlessly owing to the formation of this coating that the subsequent movement of the coats of the ovule has been hidden

from view, and has thus remained unnoticed. The assurance that such a movement must actually have taken place, is proved by the form of the raphe, and the very different position of the integuments in the ripe seed to that which they ought to have, according to the usual structural development. It is more than probable that the embryo-sac still remains immediately investing the embryo, in the *Cucurbitaceæ*, but this is not easily discernible, as there is no albumen, and as the primine and secundine, and probably also the tericine, become resolved into delicate membranes. Mirbel showed that about the period of fecundation, the embryo-sac had broken away from the ganglyode; and we must assume, in order to account for the changes that subsequently occurred, that it also separated itself afterwards at the summit from the micropyle; but if the integuments received a subsequent amount of torsion, why did not the embryo-sac, or at least the embryo, follow the same movement? What could have retained the embryo in the same position it previously held, during the second inversion of the primine and secundine? The whole of this œconomy is so extraordinary, as to call for the especial investigation of some able botanist, accustomed to accurate and delicate examination. I have simply announced the facts as I have found them, leaving it to be determined how far the hints above given, respecting the nature of these changes, may prove well-founded, or how far the whole matter may be modified by farther evidence.

The facts detailed in the preceding part of this paper clearly show, that the genus *Urandra* of Mr. Thwaites bears no relation whatever to the family of the *Olacaceæ*, and we have irresistible evidence that it differs in no respect from *Stemonurus*, with which genus it must remain, like *Gomphandra*, another of its synonyms; it agrees with it in its cupuliform, 5-toothed, persistent calyx, its five acuminate linear smooth valvate petals, its five alternate stamens, with thick filaments clothed at their summit with clavate hairs, oblong anthers somewhat divergent below, a conical ovary encircled at its base by a small annular gland, and unilocular, with two suspended ovules, a short style, and a small subcapitate stigma. The drupe and seed, as described by Mr. Thwaites, agree in every respect in their extraordinary development with what I have shown to exist in *Stemonurus*, and there is not one single feature, among those described, that I can discover, at variance with that genus. The plant of Mr. Thwaites, which appears to differ specifically from others on record, must therefore bear the name of *Stemonurus apicalis*.

The remarks of Mr. Thwaites contained in his paper above cited, relative to the Ceylon species of *Stemonurus* described by me, will form the subject of a distinct notice.

EXPLANATION OF THE FIGURES.

TAB. XIX.

- Fig. 1. Is a seed of *Stemonurus polymorphus*:—*natural size*.
- Fig. 2 & 3. The coriaceous endocarp deprived of its pulpy covering, seen on its dorsal face and on its side.
- Fig. 4. The same on its ventral face, showing the channel in which is imbedded the cord formed of the axile placentary nourishing vessels.
- Fig. 5. Is a section of fig. 3. *magnified*:—*a.* is a foramen in the summit of the channel through which the raphe passes into the cell of the putamen; *b.* the longitudinal channel in which the placentary cord is imbedded, and which passes into it through a tubular passage leading from the base.
- Fig. 6. The seed removed from fig. 5. seen on its edge:—*a.* is the free portion of the raphe by which the seed is suspended; it is a continuation of the axile placentary cord *c*; *b.* is the raphe imbedded in the integument.
- Fig. 7. The same viewed upon its dorsal face, showing the singular course of the raphe.
- Fig. 8. The same observed from above: the same letters refer to the same points in the three last figures.
- Fig. 9. The integument removed and spread out to show the form of the raphe more distinctly.
- Fig. 10. The albumen.
- Fig. 11. A transverse section of the same, showing the cavity formed by the persistent embryo-sac.
- Fig. 12. A longitudinal section of the same.
- Fig. 13. The persistent embryo-sac removed from the albumen with the embryo in its natural position.
- Fig. 14. The embryo removed.
- Fig. 15. Same still further magnified.
- Fig. 16. Is a seed of *Anona sylvatica*:—*natural size*.
- Fig. 17. The same seen sideways.
- Fig. 18. The same magnified, showing the marginal expansion of the crustaceous covering and its open cavity at the base.
- Fig. 19. One side of the cell removed, to show the enclosed seed and the hollow chamber at the base.
- Fig. 20. A transverse section of fig. 18, showing the raphe lying in a groove of the albumen along each side.
- Fig. 21. The seed removed, showing the annular form of the raphe and its connexion with the ceiling of the basal chamber of the shell: from the centre of the latter a mucronate point, as long as the hollow chamber, projects, and at each angle two threads are observed in the same space.
- Fig. 22. The same viewed edgeways, showing the peripheral form of the raphe.
- Fig. 23. The raphe separated and remaining attached to the ceiling of the basal chamber.
- Fig. 24. A longitudinal section of the albumen with the enclosed embryo.
- Fig. 25. The basal portion of the same *more highly magnified*, showing the embryo, and the hollow in the base of the albumen caused by the impression of the basal chamber.
- Fig. 26 & 27. The embryo seen in front and sideways.
- Fig. 28. A fruit of *Citrosma Aposyce*, Mart.
- Fig. 29. A seed capped by a glandular enlargement of the style.
- Fig. 30. The same deprived of its cap.
- Fig. 31. The same with its fleshy epiderm removed, showing an echinate nut.
- Fig. 32 & 33. The same magnified, seen in front and sideways, showing the flat expansion of its border.
- Fig. 34. A longitudinal section of the same, showing its hollow hilum and the enclosed seed.

- Fig. 35. The seed detached, showing the annular raphe :—*a.* commencement of the raphe at the hilum ; *b.* termination of the raphe.
- Fig. 36. The same seen edgeways.
- Fig. 37. The raphe detached :—*a.* its commencement at the hilum ; *b.* its termination at the chalaza.
- Fig. 38. Section of albumen, showing a minute embryo near its base :—*c.* relative position of embryo with the commencement *a*, and the termination *b*, of the raphe.
- Fig. 39. Base of albumen with embryo greatly magnified, the same letters referring to the same parts.
- Fig. 40. An anatropal ovule of *Cucumis Anguria* near the period of its fertilization ; after Mirbel.
- Fig. 41. The same seen just after impregnation ; also after Mirbel :—*a.* the primine ; *b.* secundine ; *c.* tercieue or nucleus ; *d.* quartine or embryo-sac suspended at the micropyle or mouth of the primine and secundine ; *e.* base of embryo-sac broken away from its attachment to the chalazal point of the tercieue ; *f.* the nascent embryo hung in the mouth of the micropyle by its suspensor ; *g.* the ganglyode or point of union of primine, secundine and tercieue, and the future chalaza ; *h.* two layers of solid cellular tissue forming a distinct coating secreted and deposited over the primine ; *i.* the raphe originating in the funicular cord, and terminating at *g*, the ganglyode or chalazal point ; *k.* a pollen-tube inserted within the micropyle.
- Fig. 42 & 43. A seed of a species of *Colocynth* from the Pampas of Buenos Ayres, seen in front and sideways.
- Fig. 44 & 45. The same magnified, showing its hollow hilum at *f*.
- Fig. 46. The same seen from below, showing the peripheral zone and the basal hilum.
- Fig. 47. A longitudinal section of the same :—*a.* the crustaceous tunic ; *b.* a nearly annular and perfectly free raphe lying between the crustaceous covering and the true integuments of the seed : it first passes through a tubular channel *c* on one side of the base of the crustaceous covering, and takes its course all round the enclosed seed, and again arrives at the base, disappearing in the loose cellular pith that fills the hollow space within the hilum ; the spiral threads appear to separate here and again unite to form a kind of suspensor to the seed ; *d.* is a reddish-coloured areole on the summit of the integument, at the spot where the chalaza should exist according to ordinary rule, but the raphe certainly does not enter or terminate here, but passes freely over it, like a bisecting line ; *e.* is another dark-coloured areole around the neck of the suspensor at the opposite extremity, which appears to unite with the raphe, for it contains spiral vessels ; *f.* is the hollow chamber within the hilum filled with loose pithy cells.
- Fig. 48. The same viewed from the summit, showing *d* the false chalaza, and the manner in which the raphe crosses it.
- Fig. 49. The raphe detached, apparently connected by very minute threads with the neck of the suspensor.
- Fig. 50. The spiral vessels of the raphe highly magnified.
- Fig. 51. The seed invested by the testa and tegmen, both very thin membranes : *d.* the false chalaza ; *e.* probably a true chalaza.
- Fig. 52. The basal termination or neck of the two investing integuments, which are distinct and separable ; the outer one is the testa ; the inner one only is marked at *e* with a dark areolar spot, from which the spiral vessels are extended, and this is probably the true chalaza.
- Fig. 53 & 54. The embryo seen in front and sideways.
- Fig. 55. The same with one of the cotyledons removed, to show its nervation.